THE DEVELOPMENT OF WINGS OF CERTAIN BEETLES, AND SOME STUDIES OF THE ORIGIN OF THE WINGS OF INSECTS.

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CONTENTS.

PLATES XI–XVII.

INTRODUCTION.

The following paper contains the result of some investigations on the development of the wings of certain beetles and of an attempt to throw some further light on the primitive origin of the wings of insects.

This work, done in the entomological laboratory of Stanford University, was begun at the suggestion of Professor V. L. Kellogg and was carried on under his supervision, and to him my heartiest thanks are due for his many helpful suggestions and the great interest he has taken in my work.

That the wings of insects with a complete metamorphosis are present in the larva was known as far back as the time of Malpighi

(1767), while the beginning of our accurate knowledge of the manner of their development was made by Weismann (1864–6). Since his time there have been many workers in this field, but most of them have worked with the Lepidoptera and Diptera — orders in which the wing development is of a very complicated type, while on the Heterometabola and the more generalized of the Holometabola as the Coleoptera and Neuroptera, much less has been done. The only extended accounts of the development of the wings in the Coleoptera are those of Comstock and Needham (1899), Kruger (1899), Needham (1900) and Tower (1903).

In this paper I have traced in detail the development of the wings of two species of Scolytidæ or engraver beetles, *Tomicus plastographus* and *Dendroctonus valens* and have added some observations made on the development of the wings of a number of other beetles, the complete history of which I was unable to obtain. I have dealt only with the development of the wings in the larva, as it is probable that there is nothing in the pupal development of the wing that differs greatly from the accounts of Tower and others, or likely to have any bearing on the origin of wings. The second part of the paper is devoted to a discussion of the several theories that have been advanced to account for the origin of the wings of insects and the bearing that my observations have on the subject.

I. THE LIFE HISTORY OF TOMICUS PLA STOGRAIHUS LEC, AND OF DENDROCTONUS VALENS HOPK.

Both these beetles belong to the family Scolytidæ and in some localities in California are so numerous that they do considerable damage to the Monterey Pine, on which they both feed.

The burrow made by the adult *T. plastographus* is some six inches in length and is three-branched, having something the shape of a Y, the entrance being at the intersection of the branches, one of which is considerably shorter than the others. The eggs are laid in little pockets along each side of the burrow and are tightly packed in with little chips of wood. In warm weather the eggs hatch in about one week. The larva bores a tunnel out at right angles to the parent gallery and becomes full grown in about two weeks. Pupation takes place in a cell at the end of the larval gallery and lasts about one week; so that a full life cycle is passed through in about four weeks. Breeding goes on continually throughout the year in this locality, but during the winter months development is much slower. There are but two moults during larval life, *T. plastographus* being rather unusual in this respect, though Needham (1900) states that the larva of the flag-weevil, *Mononychus vulpeculus* has but two moults. The larva (Fig. 32) is a white footless grub. The eyes are lacking and the antennæ are reduced to a minute knob. The spiracles have no chitinous surrounding ring and are very hard to discern.

It may be well to mention here some observations I have made on the habits of this beetle of which I have seen no record. The male is apparently polygamous in its habits. As is usual in this family the work of making the burrow is shared by both sexes. In opening the galleries I found that there were generally three adults in each gallery, one at the end of each long arm and one at the center. Dissection proved that in each case two of these are females and one a male (when it was possible to determine the sex, it being very hard to separate the sexes after oviposition had taken place). I believe that the long arms of the gallery are made by the females, while the male makes the short arm and keeps a position near the entrance to the gallery, but I was not able to get positive proof of this. In some galleries however, there were but two beetles, a male and a female; occasionally there were four adults to a gallery.

The number of eggs laid in each pocket is variable; in the majority of galleries but one egg is laid in each pocket, but in a number of galleries examined several eggs had been deposited in each pocket, the number varying from two to seven — in no case was a pocket found with only one egg in it, while in those galleries with one egg to a pocket, in no case was more than one found in each pocket. The number of beetles in the gallery had no connection with the number of eggs in the pockets.

There is considerable variation in the size and number of the projections on the tip of the elytra, but this does not seem to be a sexual variation.

Dendroctonus valens forms a large irregular gallery under the bark and the eggs are laid loosely among small chips or shavings along one side of the burrow. This species works only at the base of the trees whereas *T. plastographus* works throughout the length of the tree.

After hatching, the larvæ feed on the sides of the gallery, enlarging it in all directions. The larva moults, I think, three times, but I am not absolutely sure of this point and it is possible there are but two moults. In warm weather six to eight days elapse between each moult, the whole life cycle being passed in five to six weeks. The pupal period is passed in a cell of chips, formed in the gallery, and requires from a week to ten days.

The general appearance of the larva (Fig. 33) is much the same as the larva of *T. plastographus*, but it is larger and each spiracle is surrounded by a chitinized cresent, below which, on the abdominal segments, is a large oval chitinized disc or tubercle. There is also a strongly chitinized caudal plate on which are a number of short stout spines.

II. Development of the Wing.

1. *Formation and Growth.*

(*a*) *Early Stages.* — The wing fundament, in all the Holometabola and probably in all the Heterometabola as well, becomes first recognizable as a slight thickening of the hypodermis on the pleurum of the meso- and metathorax (Figs. 1, 2, 18). In the larvæ of *T. plastographus* and *D. valens* the cells that are destined to form the wing begin to be differentiated from the rest of the hypodermis sometime during the middle or latter part of the penultimate stage, the time of first appearance varying somewhat in different individuals. This thickening increases in size towards the end of the penultimate stage and extends the greater part of the length of the segment as an oval disc, becoming thinner on the edges and gradually merging into the hypodermis. The cells become quite crowded together and elongate and the nuclei come to lie at several levels in the disc.

Just before the last moult the outer surface of the wing disc becomes thrown up into prominent folds and ridges (Figs. 3, 23) due to the compression of the growing hypodermis by the old chitinous covering. This folding and ridging of the hypodermis takes place to a greater or less extent all over the body, but it is most pronounced in the rapidly growing cells of the wing disc. The cells of the disc are now quite long and narrow and there are traces of what later becomes very pronounced — a narrowing and elongation of the bases of the cells so that they become almost thread-like (Fig. 3). The degree of this separation, however varies in different individuals. The cytoplasm of the cells also seems to become thinner or lighter colored near the center of the inner surface of the disc. After moulting, the folds and ridges disappear from the surface of the wing disc (Fig. 6) and the hypoderm, by the expansion of the body after becoming free from the old cuticle. There does not seem to be any sudden and great proliferation of the cells of the disc just before moulting, as was found in the Lepidoptera by Verson (1904) and the growth of the wing appears to be even and constant up to the prepupal period, when it becomes accelerated.

(*b*) *Types of Wing Development.* — Tower (1903), working on the development of the wings in Coleoptera, found three types of wing development present in that order, which he designated as the simple, the recessed and the enclosed. The simple type, in which the wing merely evaginates and lies between the cuticle and the hypodermis, he found to be the prevailing type among the Coleoptera. The recessed type he found only in the Scarabæidæ. In this the disc first invaginates, then evaginates and lies in the shallow open pocket thus formed. This is the type found by Gonin in the Dipteron, *Corethra.* In the third, the enclosed type, after the invagination the opening becomes closed and the wing evaginates downward into a closed sack, formed by the lower wall of the invagination. This type was found by Tower to occur in the Coccinellidæ and the Chrysomelidæ. There are two other types, which have been found only in the Diptera, the stalked and the detached. They are similar to the enclosed type except that the walls of the invagination in the stalked type become very thin and the evaginated part, which forms the wing, is pushed well into the body cavity, while in the detached type the wing bud is entirely separated from the hypodermis and lies free in the body cavity.

In all the Coleoptera, according to Tower (1903), after the wing disc becomes well thickened, a pit-like invagination forms in the center of the disc, which rapidly widens into a groove extending nearly the length of the disc. In those insects in which the wings develop within the body, this invagination becomes much extended and the hypodermal layers thus extended form the peripodal sack into which the wing is evaginated. Tower found this primary evagination forming, even in those beetles which have a simple type of wing development. I find, however, that in both *T. plastographus* and *D. valens* this primary evagination is not formed. The only other record among Coleoptera in which the wing evaginates without this preliminary invagination is that of Needham (1900) in the flag-weevil (*Mononychus vulpeculus* Fab.).

(*c*) *Evagination of the Wing.* — During the middle of the last stage, in *T. plastographus* and *D. valens*, the evagination of the disc to form the two layers of the wing takes place. Up to this time the wing disc has been more or less convex on its outer surface and nearly straight on its inner surface and thickest in the center (Fig. 6). In the wing of an undetermined Buprestid, however, the convexity of the disc is on the inner surface (Fig. 18). The cells of the lower part of the disc now begin to elongate and push outward and downward so that the thickest part is near the lower edge (Fig. 4). At the same time there begins a slight pushing in of the cells at the lower edge of the disc (Fig. 34). Thus we have a double process going on in the formation of the wing, an evagination of the cells downward and an invagination pushing the lower edge of the disc upwards and inwards, so that the apex of the future wing is soon formed. This same process takes place in *Bruchus* sp. and in an undertermined Buprestid (Figs. 19, 20, 35, 37). Below the apex of the wing there is formed a prominent spur or projection of the hypodermis. This projection persists and is recognizable until near pupation, when the wing begins to elongate greatly and become folded under the cuticle. The bases of the cells near the center of the disc now become greatly narrowed and separated from each other, soon becoming almost thread-like. These narrowed bases become quite distinctly demarcated from the rest of the cells and the nuclei, since they taper quite abruptly so that a wing at the stage shown in Fig. 38 appears at the first glance to have a large lumen, but a careful examination shows that, in *T. plastographus* and *D. valens* as well as in several other beetles examined, the basement membranes of the two sides of the wing are more or less closely pressed together, though not fused. During the early stages of the formation of the evagination, the basement membrane sinks in near the center of the disc, then becomes folded on itself and pushes out into the elongated bases of the cells as a double sheet extending nearly the length of the disc. The different stages of the elongation and narrowing of the cells and the formation of the wing cavity by the evagination of the basement membrane into the disc, coincident with the pushing downward of the apex of the wing can be seen in Figs. 7, 19, 35, 36, 38. Fig. 38 shows the stage of development reached by the wing about the beginning of the prepupal period, at which time tracheæ and tracheoles begin to push into the wing and the vein cavities are formed. This method of development of the wing, though described from *T. plastographus* applies equally well to the Bruchidæ (*Bruchus* sp.) and to certain of the Buprestidæ as well as to *D. valens*.

With the growth of the wing downward there is a corresponding pushing upward of the invagination at the lower edge thus bringing the wing outside the body, between the hypoderm and the cuticle, while the increase in the size of the body keeps pace with the growth of the wing, so that, although the wing is constantly growing downward and increasing in length, it does not push past the spur or projection in the hypoderm below it until that disappears by the stretching of the hypoderm, late in the prepupal period.

(*To be continued.*)

Class I, HEXAPODA.

Order IV, DIPTERA.

BRIEF NOTES ON MOSQUITO LARVÆ.

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LARVA OF ANOPHELES BARBERI COQ. — Mr. H. S. Barber originally obtained eggs of this species at Plummer's Island, Md., and turned them over to the Bureau of Entomology, from whence I received them and carried one to the last stage. This was late in the fall and the larvæ were lost over winter. Their actual occurrence was unknown to us. Last summer Mr. F. C. Pratt had the good fortune to discover the larvæ in water in hollow trees at Trapp, Loudon Co., Va. (July 25, 1904). They were taken in charge by Mr. F. Knab, who informs me that in addition to feeding with the mouth brushes in the usual way, the larvæ were predacious, seizing *Culex* larvæ with great activity. This remarkable habit for a larva that can exist on a vegetable diet was observed both by Mr. Knab and Mr. Caudell. Their natural prey are apparently the larvæ of *Culex triseriatus*, *C. signifer* and *C. restuans*, the first two of which inhabit normally hollow trees, the last has been so found by Mr. Pratt.